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Effect of trophic status and sediment particle size on diversity and abundance of aquatic Oligochaeta (Annelida) in neotropical reservoirs

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Abstract – The influence of the sediment grain size and the trophic status of the reservoirs on the composition, richness and biomass of Oligochaeta community was tested. Samples were taken from the littoral and profundal zones of 30 neotropical reservoirs from six different watersheds during two hydrological periods (dry and rainy seasons). The sample units were ordinated, with principal component analyses, according to differences in the sediment grain size, sample depth and dissolved oxygen. The results of a multiple response permutation procedure (MRPP) analysis revealed significant differences in species composition between littoral and profundal zones, trophic status (oligotrophic, mesotrophic and eutrophic) and different watersheds. The environment–species relationship was tested using redundancy analyses. In order to test which environmental variables, either granulometric or limnological, influenced the Oligochaeta community variability we used a partitioning procedure of inertia. Local variations, including reservoir zone and trophic status, were primarily influenced by differences in sediment type and depth. Significant differences in the total biomass between zones, trophic status, watershed and hydrological period were also demonstrated by a Kruskal–Wallis or Mann–Whitney test. The most prevalent taxa were the cosmopolitan tubificids *Bothrioneurum* sp. and *Branchiura sowerbyi*, and the naidids *Dero* (*Dero*) *digitata* and *Pristina breviseta*, which are dependent on periphyton for food. Higher biomass values were recorded in mesotrophic reservoirs, due to increased nutrient availability and adequate dissolved oxygen supply. Our results indicate that the Oligochaete community structure is directly influenced by local environmental variation in neotropical reservoirs; and that the sediment grain size is the most important factor in determining the Oligochaete community structure.

Key words: Oligochaeta / richness / biomass / bioindicator / lentic water

Introduction

The classification of an environment according to its trophic status is an useful tool for managing lakes, and this can be estimated by simple measures of primary productivity, water transparency and nutrient concentration (Lind *et al*., 1993). These measures are important, because there is a link between nutrient supply, productivity and biological changes in aquatic ecosystems (Harper, 1992).

Alterations of the original environment, including changes to physical, chemical and biological aspects of the water body are the primary effects observed when reservoirs are created (Margalef, 1994; Matsumura-Tundisi *et al*., 2006). The principal consequences of these environmental changes are modifications to nutrient input and biological productivity, resulting in an environment with modified trophic status, generally classified as oligotrophic, mesotrophic and eutrophic.

Eutrophication can be a naturally occurring process in ageing lakes, but human activities can accelerate the rate at which nutrients enter aquatic ecosystems from the surrounding catchment areas (Harper, 1992; Menetrey *et al*., 2005). Following these changes, the eutrophication process is perhaps the most harmful effect resulting from reservoir construction, since it directly impacts the biological communities living in these environments (Rocha *et al*., 2006).

Benthic macroinvertebrates communities are related to nutrient concentrations and habitat conditions (Weijters *et al*., 2009; Friberg, 2010). Indeed, they have

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*Corresponding author: `yara.moretto@gmail.com` been used as bioindicators since their presence is indicative of water quality, particularly after alterations to the environment (Verdonschot, 1989). Consequently, there has been considerable research interest in biomass and production of benthic macroinvertebrates communities (Benke *et al.*, 1999; Bagatini *et al.*, 2007; Takahashi *et al.*, 2008). They also play an important role in trophic interactions and energy flow through aquatic ecosystems (Benke *et al.*, 1999).

Oligochaeta are one of the most abundant and diverse groups in benthic communities of rivers (Marchese and Ezcurra de Drago, 2006), streams (Alves and Lucca, 2000; Alves *et al.*, 2006), lakes (Peralta *et al.*, 2002) and reservoirs (Real and Prat, 1992; Dornfeld *et al.*, 2006). The biomass of these organisms constitutes an important link in the trophic web, since they represent an important food source for fish and invertebrates (Lafont, 1987). Owing to their low mobility, long life cycle and direct contact with the substrate, aquatic worms have an intimate relationship with local environmental conditions (Alves and Lucca, 2000) and could be related mainly to the sediment type and conditions (Bletter *et al.*, 2008, Martins *et al.*, 2011). Since they are directly influenced by sediment characteristics, oligochaetes are one of the most informative taxonomic groups in studies of pollution (Chapman, 2001; Marchese and Ezcurra de Drago, 2006).

Here, we investigate the relevance of a number of local abiotic factors, related to water chemistry as well as to sediment type, zones and trophic levels; and regional factors such as hydrological periods and watersheds on the Oligochaeta community structure of 30 southern Brazilian reservoirs. We test the following hypotheses: (1) the composition, richness and abundance of Oligochaeta are affected by trophic status of the reservoirs, so we expect positive correlation between trophic status and biomass, and negative correlation with specific richness; (2) the composition, richness and abundance of Oligochaeta communities are determined by sediment grain size, so higher diversity and abundance are expected in reservoirs with predominance of larger sediment particles (see definition below).

Material and methods

Study area

We studied 30 neotropical reservoirs from six different watersheds: Piquiri, Ivaí, Tibagi, Iguaçu, Paranapanema and Litorânea. These locations are distributed across the Paraná State, from the Serra do Mar (sea mountain range and coastal region) to the northern regions, and include reservoirs located in the border between Paraná and São Paulo states (Julio *et al.*, 2005) (Fig. 1). The studied reservoirs represent a range of environments with differing drainage areas, depths, morphometrics, ages and hydrological period. Furthermore, these locations represent various degrees of limnological characteristics and anthropogenic influences, in particular electric power generation, public water supply and tourism (Julio *et al.*, 2005).

Sampling procedure

Oligochaeta sampling was performed in July (dry season) and November (rainy season) of 2001 in the littoral and profundal zones, close to the dams, from 30 reservoirs using a modified Petersen grab (0.0180 m^2). In each station, we obtained three samples for biological analysis and one for analysis of granulometry and organic matter content of the sediment.

The samples were pre-sorted in a graded sieve system (with mesh sizes 2, 1 and 0.2 mm). The material collected in the smallest mesh was preserved in 4% formaldehyde, buffered with calcium carbonate (Bagatini *et al.*, 2007) and later sorted using stereoscopic microscopy. All organisms found in different mesh sizes were preserved in buffered 4% formaldehyde.

Oligochaeta were identified to the most precise taxonomic level possible, using identification guides from Brinkhurst and Marchese (1992). After identification, organisms were rinsed in distilled water for one hour to remove excess formaldehyde. Specimens were then dried at 60 °C for 24 h, cooled in desiccator and weighed on a microscale with 10^{-7} g precision (Sartorius Ultramicro). The biomass of each species was recorded in milligrams of dry weight per square metre ($mg.m^{-2}$).

The measured environmental variables included water temperature, pH (pHmeter-Digimed), electric conductivity (condutivimeter Digimed) and dissolved oxygen (oxymeter-YSI). All variables were measured close to the bottom of the littoral and profundal zones of the reservoirs. To determine the granulometric composition of the sediment, we used the Wentworth scale (Wentworth, 1922). According to Suguio (1973), the size of sediment grain is classified as pebbles (4.00 mm), granules (2.00 mm), very coarse sand (1.00 mm), coarse sand (0.50 mm), medium sand (0.25 mm), fine sand (0.12 mm), very fine sand (0.63 mm) and mud (<0.63 mm). The percentage of organic matter in sediment was estimated through sub-sample burning in a muffle furnace at 560 °C for 4 h.

Statistical analysis

Principal component analyses (PCA) were performed to discriminate the distribution pattern of the sample units based on environmental variables (water temperature, dissolved oxygen, pH, electrical conductivity, sediment type and organic matter) from littoral and profundal zones of the reservoirs. All these data (except pH) were log transformed, and PCA axes were selected according to Broken–Stick criteria (Jackson, 1993).

The trophic status index (TSI) of Carlson (1977), modified by Toledo *et al.* (1983), was used to characterize the trophic status of the reservoirs.

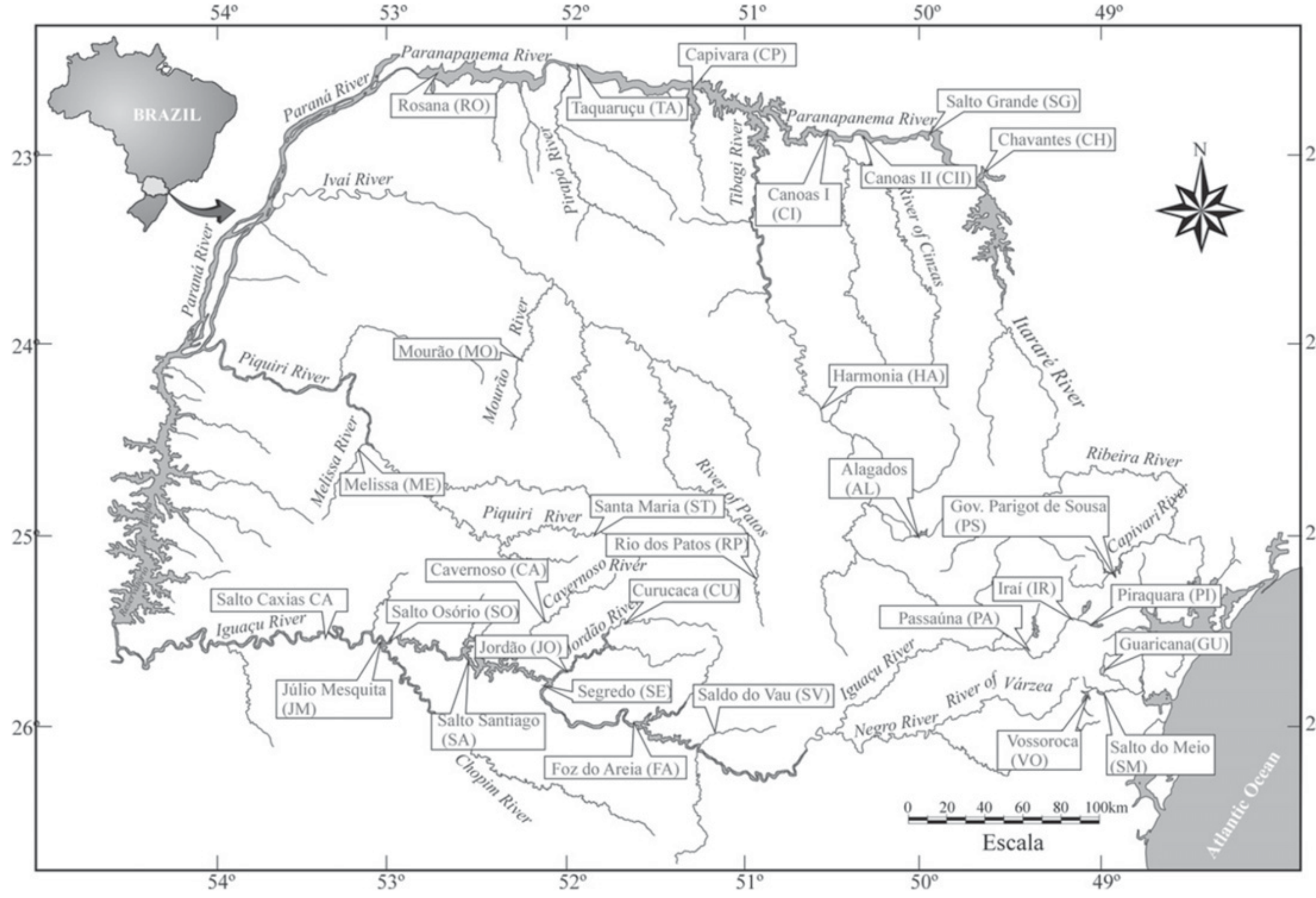

Fig. 1. Location of the 30 reservoirs of Paraná state.

The difference in Oligochaeta species composition was further tested with respect to differences between zones, including hydrological period, trophic status and watersheds, through a multiple response permutation procedure (MRPP). This is a non-parametric procedure based on Sørensen distance, which tests for differences in the assemblage structure among previously defined groups (Zimmerman *et al.*, 1985).

A non-parametric ANOVA (Kruskal–Wallis) or Mann–Whitney was performed to test for possible differences in species richness and biomass of Oligochaeta, among zones, hydrological periods, trophic status and watersheds. Since the homoscedasticity assumption was not accepted for the analysed attributes, a parametric ANOVA could not be performed.

The environment–species relationship was tested using redundancy analyses (RDA) with a Hellinger transformation to the abiotic data matrix and the standardized environmental variables (root square). The global significance of the RDA axes was analysed by a permutation test (Legendre *et al.*, 2011). To observe which environmental variables, granulometric or limnological, influenced variability among Oligochaeta community, we used a partitioning procedure of inertia (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006).

The Kruskal–Wallis non-parametric ANOVA and the Mann–Whitney test were performed using Statistical software version 7.1 (Stat Soft Inc., 2005) and PCA and MRPP were performed using PC-ORD software (McCune and Mefford, 1999). RDAs were developed with R software version 2.14.1 (R Core Team, 2011) using the VEGAN package (Oksanen *et al.*, 2011).

Results

Abiotic variables

Mean water temperature ranged from 16.10 to 24.10 °C in the littoral zone of reservoirs, while in the profundal zone, values ranged from 12.30 to 22.70 °C. Higher depths were measured in profundal zones (3.70–135.00 m) than in littoral zones, which were shallower (0.45–6.75 m), except to Salto Santiago reservoir (30.00 m) and Salto Caxias (27.00 m). In these reservoirs, it was not possible to sample close to the shore because of the abundant presence of submerged trees. The mean pH values in the littoral (6.20–8.30) and the profundal (5.10–8.20) zones generally showed little variation, but significant variation was observed in electrical conductivity and dissolved oxygen concentration in the two zones. Electrical conductivity values ranged from 21.15 to 126.8 μS.cm^{-1} in the littoral zone and 21.55 to 141.80 μS.cm^{-1} in the profundal zone of the reservoirs. Lower values of dissolved oxygen were

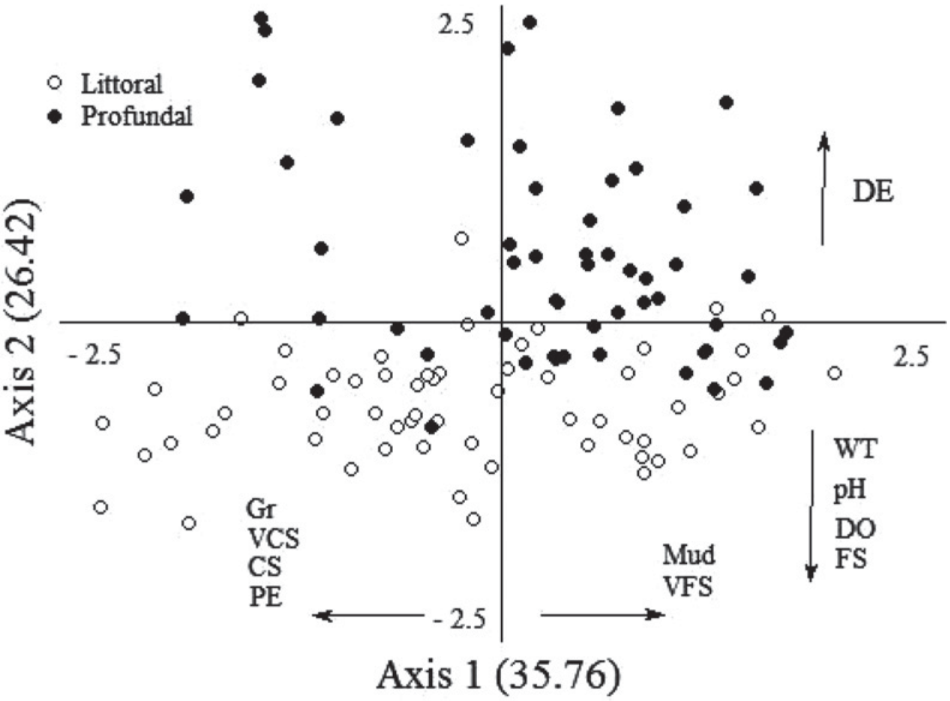

Fig. 2. Score distribution of PCA derived from physical and chemical variables of water and sediment. (WT, water temperature; DO, dissolved oxygen; DE, depth; Gr, granule; VCS, very coarse sand; CS, coarse sand; PE, pebbles; VFS, very fine sand.)

recorded in the profundal zone (0.04–8.50 mg.L^{-1}), whereas higher values (6.20–10.00 mg.L^{-1}) were recorded in the littoral zone. Organic matter content varied between 1.90% and 38.80% in the littoral zone and between 1.70% and 53.50% in the profundal zone. The sediment composition of the reservoirs was generally composed of a range of particles, ranging from 0.63 to 4.00 mm (see Appendices 1 and 2).

Regarding abiotic variables, PC1 showed that differences between reservoirs are due primarily to differences in sediment texture (Fig. 2). Reservoirs dominated by large sediment particles (granule, very coarse sand, coarse sand and pebbles) were negatively correlated with this axis, whereas reservoirs with sediment primarily composed of fine particles (mainly mud and very fine sand) were positively correlated. Differences between reservoir zones (littoral and profundal) in axis 2 were explored. The littoral zones characterized by shallower depths and higher values of water temperature, pH, dissolved oxygen and higher percentages of fine sediment, were negatively correlated to axis 2, while depth was positively correlated (Fig. 2).

The trophic status of reservoirs varied according to the hydrological period (rainy and dry seasons), as indicated by the values of the TSI. Most of the reservoirs were classified as oligotrophic in both hydrological periods. Moreover, the reservoirs Melissa (ME), Rio dos Patos (RP), Passaúna (PA) and Salto do Meio (SM), which were considered oligotrophic during the dry season, were classified as mesotrophic in the rainy season, while the Julio Mesquita Filho (JM) reservoir changed from oligotrophic in the dry season to eutrophic in the rainy season. Only the Iraí (IR) reservoir was classified as eutrophic in both periods (Table 1).

Composition

Sixteen species of Oligochaeta were found in the present survey, and these are distributed in six families (Enchytraeidae, Opistocystidae, Naididae, Tubificidae, Narapidae and Alluroididae). Twelve of these taxa belong to families Tubificidae and Naididae, with six taxa in each family. The absence of mature specimens of *Bothrioneurum* and some *Aulodrilus* precluded specific identification of these genera. The most common species were *Opistocysta funiculus, Pristina breviseta, Dero (Dero) digitata, Stephensoniana trivandrana, Aulodrilus pigueti* and *Bothrioneurum* sp. in the studied reservoirs (Table 2).

The Enchytraeidae (non-identified – NI) *Pristina americana* and *Aulodrilus* sp. occurred only in the littoral zones, while Tubificidae (NI) was found in the profundal zones only. The composition of the oligochaete communities was similar in both hydrological periods. Significant differences in composition were observed among reservoirs with different trophic states. All 16 taxa were recorded in the oligotrophic reservoirs and Enchytraeidae (NI), *Pristinella longisoma*, *Aulodrilus* sp., *Branchiura sowerbyi*, *Narapa bonettoi* and *Brinkhurstia americanus* were absent from mesotrophic and eutrophic reservoirs. *P. americana*, *D.* (*D.*) *digitata*, *Dero* (*Aulophorus*) *borellii*, *Limnodrilus hoffmeisteri* and *Bothrioneurum* sp. occurred in mesotrophic reservoirs and did not appear in the eutrophic reservoirs. Only four oligochaete species, *O. funiculus*,

Table 1. Carlson Trophic Index modified by Toledo (1983) for 30 neotropical reservoirs. (TSI, trophic status index; TSC, trophic status category; D, dry period; R, rainy period; OL, oligotrophic reservoir; ME, mesotrophic reservoir; EU, eutrophic reservoir. The names and codes of the reservoirs are in Fig. 1.)

	TSI		TSC			TSI		TSC	
Reservoirs	D	R	D	R	Reservoirs	D	R	D	R
ST	27.4	41.5	OL	OL	SE	43.6	35.8	OL	OL
ME	43.0	50.2	OL	ME	FA	39.0	39.5	OL	OL
MO	38.4	38.9	OL	OL	OS	35.5	37.6	OL	OL
RP	40.8	44.9	OL	ME	CU	31.8	29.2	OL	OL
HA	42.9	41.8	OL	OL	CH	27.7	36.7	OL	OL
AL	42.2	41.9	OL	OL	SG	35.7	31.7	OL	OL
JM	41.1	54.8	OL	EU	CP	38.0	34.3	OL	OL
SA	31.6	39.5	OL	OL	CII	40.7	40.1	OL	OL
CA	34.7	42.2	OL	OL	CI	38.9	36.1	OL	OL
PI	30.5	33.4	OL	OL	TA	39.7	36.5	OL	OL
IR	57.4	63.6	EU	EU	RO	41.8	33.5	OL	OL
PA	30.5	46.8	OL	ME	PS	35.0	35.3	OL	OL
JO	29.5	27.4	OL	OL	VO	31.8	34.3	OL	OL
SV	25.8	28.2	OL	OL	SM	40.0	45.5	OL	ME
CV	29.4	37.6	OL	OL	GU	43.3	36.9	OL	OL

Table 2. Species composition and mean biomass of Oligochaeta in neotropical reservoirs in different zones, trophic status and watersheds. (L, littoral zone; P, profundal zone; D, dry period; R, rainy period; O, oligotrophic reservoir; M, mesotrophic reservoir; E, eutrophic reservoir; Pi, Piquiri watershed; Iv, Ivaí watershed; Ti, Tibagi watershed; Ig, Iguaçu watershed; Pa, Paranapanema watershed; Li, Litorânea watershed.)

	Zones		Periods		Trophic state			Watersheds					
	L	P	D	R	O	M	E	PI	IV	TI	IG	PA	LI
Enchytraeidae													
Enchytraeidae (NI)	·		·		·						·	·	
Opistocystidae													
Opistocysta funiculus Cordero, 1948	·	·	·	·	·		·	·	·	·	·	·	·
Naididae													
Pristina breviseta Bourne, 1891	·	·	·	·	·		·	·	·	·	·	·	·
Pristina americana Cernosvitov, 1937	·		·	·	·	·							·
Dero (*Dero*) *digitata* (Müller, 1773)	●	·	●	·	●	·			·	·	●		·
Dero (*Aulophorus*) *borellii* Michaelsen, 1900	·	·	·	·	·	·						·	
Stephensoniana trivandrana (Aiyer, 1926)	·	·	·	·	·		·	·	·		·	·	·
Pristinella longisoma Harman, 1977	·	·	·	·	·						·	·	·
Tubificidae													
Limnodrilus hoffmeisteri Claparede, 1862	·	·	·	·	·	·					·		·
Aulodrilus pigueti Kowalewski, 1914	·	·	·	·	·		·	·	·		·	·	·
Aulodrilus sp.	·		·	·	·						·		·
Bothrioneurum sp.	●	⬤	●	⬤	⬤	●		·	⬤	·	●	●	⬤
Branchiura sowerbyi Beddard, 1892	●	●	·	·	·						·	⬤	·
Narapidae													
Narapa bonettoi Righi & Varela, 1983	·	·	·	·	·						·	·	
Tubificidae (NI)		·	·	·	·	·				·		·	·
Alluroididae													
Brinkhurstia americanus Brinkhurst, 1964	·	·	·	·	·				·		·		·

Biomass: · < 1000 $mg.m^{-2}$, ● 1000–5000 $mg.m^{-2}$, ⬤ > 5000 $mg.m^{-2}$.

P. breviseta, *S. trivandrana* and *A. pigueti*, were found in the eutrophic reservoirs, these taxa did not occur in the mesotrophic reservoirs. *Opistocysta funiculus*, *P. breviseta* and *Bothrioneurum* sp. were recorded in all six watersheds; on the other hand some species, *e.g.*, *P. americana* and *D.* (*A.*) *borellii* were exclusive to the Litorânea and Paranapanema watersheds, respectively. Enchytraeidae (NI) and *N. bonettoi* were observed in the Iguaçu and Paranapanema watersheds, and the tubificids *L. hoffmeisteri* and *Aulodrilus* sp. in Iguaçu and Litorânea (Table 2).

According to the MRPP, the Oligochaeta composition differed significantly between littoral and profundal zones ($A = 0.004$; $T = -1.943$; $P = 0.049$), among trophic status ($A = 0.011$; $T = -3.344$; $P = 0.006$) and among watersheds ($A = 0.070$; $T = -13.440$; $P = 0.000$). However, this difference was not significant for the two hydrological periods ($A = 0.003$; $T = -0.163$; $P = 0.351$).

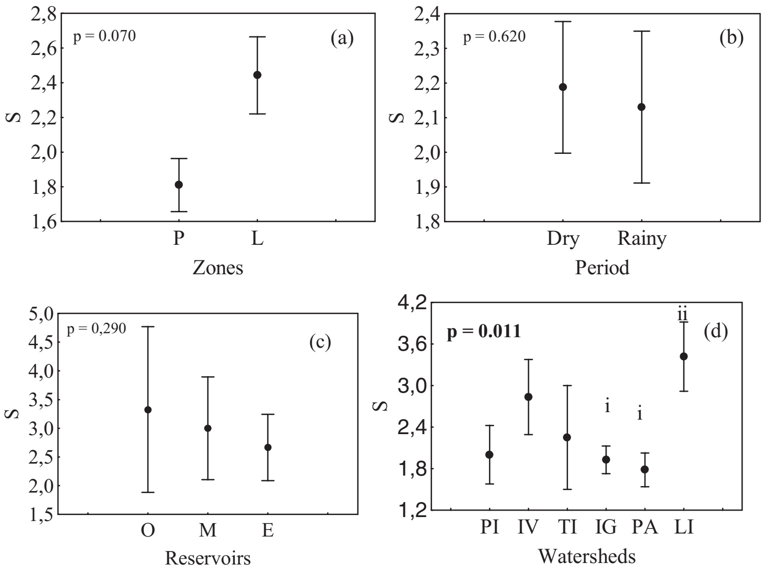

Fig. 3. Mean values and standard error of species richness (S) in different zones (a), hydrological periods (b), trophic status (c) and watersheds (d). (P, profundal zone; L, littoral zone; PI, Piquiri watershed; IV, Ivaí watershed; TI, Tibagi watershed; IG, Iguaçu watershed; PA, Paranapanema watershed; LI, Litorânea watershed.)

Species richness

The mean species richness of Oligochaeta was higher in the littoral zone (Mann–Whitney, $P = 0.070$) and in the dry seasons (Figs. 3a and b). Considering the trophic status, the richness values were similar among the reservoirs with higher values in the oligotrophic reservoirs (Fig. 3c), but the difference was not significant (Kruskal–Wallis $P > 0.05$). The richness was higher in Litorânea and Ivaí watersheds (Fig. 3d), and this difference was significant between the Litorânea watershed and the Iguaçu and Paranapanema watersheds (Kruskal–Wallis, $P = 0.006$).

Biomass

Specific biomass was higher (> 5000 mg.m^{-2}) in *Bothrioneurum* sp. and *B. sowerbyi*. These average values were observed in the profundal zone (8988.628 mg.m^{-2}), during the rainy season, in oligotrophic reservoirs and in the Ivaí and Litorânea watersheds for *Bothrioneurum* sp., and only in the Paranapanema watershed for *B. sowerbyi*. *Dero* (*Dero*) *digitata* was also quite abundant (with biomass between 1000 and 5000 mg.m^{-2}) mainly in the littoral zone (2098.367 mg.m^{-2}) and during the rainy season. Considering the trophic status of the reservoirs and the watersheds, higher biomass was observed in oligotrophic ones and Iguaçu watershed. The biomass of other species was below 1000 mg.m^{-2} (Table 2).

The higher mean oligochaete biomass, mainly of *Bothrioneurum* sp. and *Branchiura sowerbyi* (Table 2), was observed in the profundal zone (321.830 mg.m^{-2}) (Fig. 4a). Higher mean values of biomass were recorded in the dry season (184.630 mg.m^{-2}) (Fig. 4b) with higher biomasses mostly occurring in *D.*(*D.*) *digitata* and *Bothrioneurum* sp. (Table 2). Considering the trophic status and watersheds, the biomass was higher in mesotrophic reservoirs (2048.280 mg.m^{-2}) and in the Litorânea (671.840 mg.m^{-2}) and Ivaí (456.870 mg.m^{-2}) watersheds (Figs. 4c and d). Highest biomass was represented by *Bothrioneurum* sp. in the mesotrophic reservoirs and in both watersheds (Table 2).

Biomass differed between zones (Mann–Whitney; $U = 13\,116$; $P = 0.001$), hydrological periods (Mann–Whitney; $U = 14\,030$; $P = 0.027$), trophic status (Kruskal–Wallis; $H = 6.630$; $P = 0.0363$) and watersheds (Kruskal–Wallis; $H = 21.880$; $P = 0.0006$), where the Litorânea watershed differed significantly from the Tibagi and Iguaçu watersheds (Fig. 4d).

Species–environment relationship

Water temperature, pH, conductivity and trophic state index were the most important to describe the oligochaete communities gradients (Fig. 5a). As regards sediment type, granules, very coarse sand, medium sand, mud and sediment organic matter were most important to characterize the community composition of oligochaetes (Fig. 5b).

Some environmental variables showed recurrent associations with individual species. The trophic state index was positively correlated with *O. funiculus* in littoral areas, but correlated negatively with *N. bonettoi*. Electrical conductivity was an important variable during the rainy season and was positively correlated with *B. sowerbyi*. Water temperature was positively correlated with *N. bonettoi* and negatively with *Bothrioneurum*. *Bothrioneurum* was negatively correlated with pH in all RDAs performed.

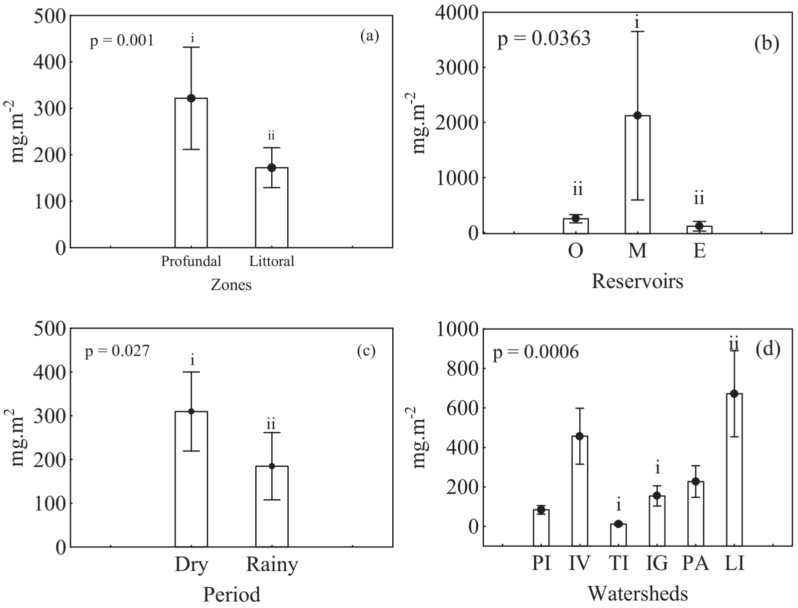

Fig. 4. Mean values and standard error of Oligochaeta biomass (mg.m^{-2}) according to zones (a), trophic status (b), hydrological period (c) and watersheds (d). (Different codes (i and ii) indicate significant differences.)

Sediment type correlated positively with the species *N. bonettoi*, *D. digitata* and *P. breviseta*, while it was negatively correlated with *B. sowerbyi*, *O. funiculus*, *P. longisoma* and *Bothrioneurum*.

The abiotic and sedimentological variables explained 57 and 80%, respectively, of Oligochaeta community variation. In inertia partitioning, the sedimentological fraction was more important to the community structure, mainly during the dry period, where the sediment explained 41 and 38% of data variability (littoral and profundal zone, respectively) and the abiotic data explained 18 and 20% (littoral and profundal zone, respectively) (Fig. 6).

Discussion

Our results showed that, in the 30 reservoirs studied, sediment type was the main driver of the Oligochaeta community composition, richness and biomass. Several other local factors, including variation in depth and in dissolved oxygen content also influenced the Oligochaeta community structure. Less pronounced was the effect of regional factors related to hydrological period and watersheds, as observed in the PCA.

The influence of local and regional factors driving species diversity has been recently discussed in different biological communities (Bini *et al.*, 2003; Stendera and Johnson, 2005; Johnson *et al.*, 2007). Studies describing assemblages of benthic macroinvertebrates have observed that local processes may be more important for the structure of these communities than regional processes (Stendera and Johnson, 2005; Johnson *et al.*, 2007), and the factors may indeed be independent (Johnson and Goedkoop, 2002). With respect to Oligochaeta, variations in species composition related to different regional and local scales have been referred in several studies (Särkkä, 1992; Real and Prat, 1992, Alves *et al.*, 2008). Changes in the characteristics of limnology and sediment observed at both local (zones and trophic status) and regional scales (watersheds and periods) significantly influence species richness and biomass of Oligochaeta in our study.

The environmental conditions of the littoral zone are favourable to a large number of invertebrate taxa (Moretto *et al.*, 2003) including Oligochaeta (Dornfeld *et al.*, 2006). The presence of larger sediment particles (pebbles and granules) and water temperature, in some reservoirs, contributed to increases in species richness as well as to the presence of the naidids *D.* (*D.*) *digitata* and *P. breviseta*. According to Erséus *et al.* (2005), *Dero* is a genus characteristic of warmer conditions, as observed in neotropical regions.

The total biomass of Oligochaeta and the tubificid *Bothrioneurum* sp. increased in the littoral zone, in both shallow and deep littoral zones (see Appendices 1 and 2), with higher concentrations of dissolved oxygen. Some studies have stated that the depth exerts a significant effect on invertebrate biomass (Martinez-Anselmi and Prat, 1984, Särkkä, 1992, Verneaux and Aleya, 1998). According to Särkkä (1992), the environmental requirements of different Oligochaeta species could be related to several depths in the environments. Similar results were described by Verneaux and Aleya (1998) on Chironomidae fauna from environments with a distinct trophic status. These authors showed the efficiency and importance of bathymetric studies in characterizing environmental preferences of organisms, and describing community variation with depth.

Tubificidae and Naididae were among the most abundant groups in Oligochaeta communities of several

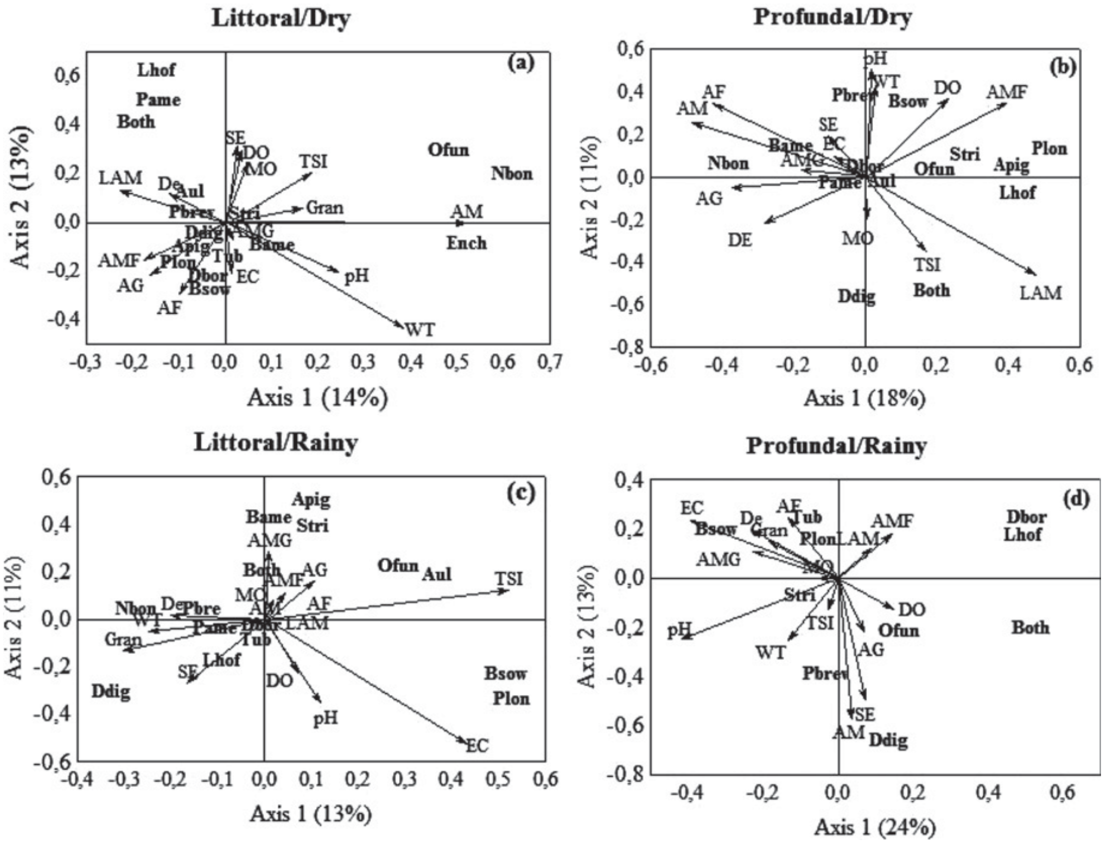

Fig. 5. Biplot species–environment of each redundancy analysis in reservoirs of Paraná state, Brazil. (a) Littoral zone/rainy period, (b) littoral zone/dry period, (c) profundal zone/rainy period and (d) profundal zone/dry period.

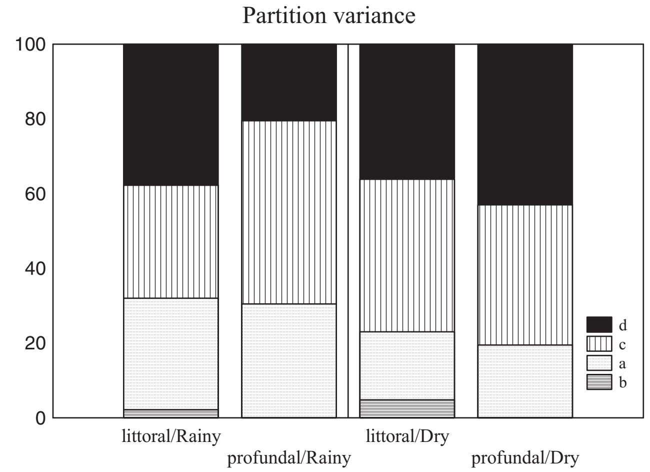

Fig. 6. Inertia partitioning showing the importance of limnological and sediment predictors to the community structure of Oligochaeta in reservoirs of Paraná state, Brazil. (Variation explained by: a, limnology; b, granulometric texture; c, interaction between limnology and granulometric texture; d, environmental data.)

aquatic ecosystems, consistent with several previous studies (Chauvet *et al.*, 1993; Alves and Lucca, 2000; Peralta *et al.*, 2002; Dornfeld *et al.*, 2006; Martins *et al.*, 2011). Tubificidae may have higher biomass compared with Naididae, simply because they are larger. *Bothrioneurum* sp. has a cosmopolitan distribution (Schenková *et al.*, 2006) and has been able to colonize a wide variety of environments, whereas the presence of naidids depends on periphyton availability (Sporka, 1996). In littoral zones, where light penetration is high, periphyton communities are more common (Rodrigues *et al.*, 2005b). Hence, these regions are favourable for naidid development (Verdonschot, 1989) and are thus able to support a higher diversity of naidid taxa. Furthermore, reservoirs with decreased concentrations of organic matter and larger sediment particles were associated with *Dero* and particularly with *Pristina* (Schenková *et al.*, 2001).

In general, the profundal zone was characterized by higher concentrations of organic matter, except in reservoirs with fine sediment. The higher mean Oligochaeta biomass in the profundal zone was primarily related to the presence of mud (direct and significant correlation between these variables). Tubificidae were the most abundant taxa and included *Bothrioneurum* sp., *B. sowerbyi* and *L. hoffmeisteri*. This family is known to live in organically enriched environments with fine sediment particles (Schenková *et al.*, 2001; Dornfeld *et al.*, 2006). The preference for this type of habitat may be due to the fact that most tubificids feed on bacteria and organic matter (Verdonschot, 1989; Rîsnoveanu and Vădineanu, 2003), both of which are available more in the profundal zones

(Peralta *et al.*, 2002; Van Duinen *et al.*, 2006). A study performed in Lake Baikal showed that food availability was a limiting factor for Oligochaeta distribution in deep regions of the lake (Martin *et al.*, 1999). Furthermore, Schenková *et al.* (2006) demonstrated that *Bothrioneurum vejdovskyanum* showed a preference for habitats with little water level fluctuation and low substrate turnover. These features are typical of lentic environments, including some reservoirs.

Oligochaeta species can be abundant in deep zones of aquatic environments (Real and Prat, 1992; Martin, 1996; Bonomi and Pasteris, 2006; Dornfeld *et al.*, 2006) since they present adaptations allowing them to survive in less favourable conditions. Gills and respiratory appendages allow some species to survive in environments where oxygen is limited (Martin, 1996; Raposeiro *et al.*, 2009). An example is the tubificid *B. sowerbyi* and the naidid *D.* (*A.*) *borelli*, both of which present respiratory appendages and are abundant in deeper reservoirs where the oxygen levels were generally low. A study carried out by Martinez-Anselmi and Prat (1984), in 63 Spanish reservoirs, showed that the depth was not a critical factor for Oligochaeta species and that Naididae in particular are able to survive at considerable depths in reservoirs, since oxygen levels close to the bottom were sufficient for these species.

The trophic status of reservoirs, as well as its geographic distribution over the watersheds, contributed to differences in the Oligochaeta community structure. In general, species diversity and biomass were higher in mesotrophic reservoirs. The higher nutrient concentrations of these environments contributed to an increase in primary productivity of phytoplankton and periphyton (Rodrigues *et al.*, 2005a, 2005b) as well as of bacteria (Pagioro *et al.*, 2005), which subsequently increases food resource to the macroinvertebrates. Colonizing experiments emphasized that Oligochaeta are important to the detritivorous food chain, because they have distinct abilities to exploit different food sources (Martins *et al.*, 2011).

The increase in the productivity associated with higher nutrient input generally stimulates increasing species abundance, until the dissolved oxygen supply has been entirely consumed. In the profundal zone of a eutrophic reservoir (Iraí reservoir), we recorded low concentrations of dissolved oxygen, while, in the mesotrophic reservoirs, the oxygen supply was higher. This fact could explain the increased biomass associated with mesotrophic reservoirs as compared with eutrophic reservoirs. Mesotrophic reservoirs contained adequate levels of dissolved oxygen, which may support increased biomass, and species richness.

The location of mesotrophic reservoirs in the Litorânea watershed accounts for elevated species diversity of the Oligochaeta community. The Litorânea watershed is isolated in the Sea Mountain Range and, consequently, has less anthropogenic influence compared with the other watersheds. This fact may contribute to higher biomass and diversity of the associated community.

Different methods have been used to describe invertebrate communities in the context of environmental trophic status (Saether, 1979; Real and Prat, 1992; Verneaux and Aleya, 1998; Takahashi *et al.*, 2008). Oligochaeta has been used successfully in trophic classifications (Slepukhina, 1984; Verdonschot, 1989; Rossaro *et al.*, 2006). Nevertheless, a study carried out by Lafont (1984) reported some difficulties in the use of Oligochaeta as a tool to evaluate the impact of human activities on aquatic ecosystems, since each habitat category contributes to the dynamics of this group. Moreover, several authors have shown that the organisms will not always be reliable indicators of environmental conditions (Saether, 1979; Lafont, 1984; Verdonschot, 1989; Verneaux and Aleya, 1998).

In conclusion, the composition, richness and biomass of Oligochaeta communities in neotropical reservoirs were directly influenced by local environmental variation. We were able to corroborate our initial hypothesis that sediment grain size is the most important factor determining the Oligochaete community structure. Depth also contributes to the local community structure. The results obtained in the present study also showed a significant influence of trophic status on diversity and biomass of the Oligochaeta class, confirming our (second) hypothesis that low species richness is sustained in most trophic reservoirs. Mesotrophic environments, however, were more favourable to communities in terms of biomass, contrary to our initial hypothesis.

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Appendix 1. Mean values, standard deviation (between parentheses), minimum and maximum of the physical and chemical variables of the water and sediment and organic content in the littoral zones of the reservoirs. O, Oligotrophic; M, Mesotrophic; E, Eutrophic.

Reservoirs littoral	Period		Water temperature (°C)	Depth (m)	pH	Electrical conductivity (μS.cm^{-1})	Dissolved oxygen (mg.L^{-1})	Organic content (%)	Sediment (> %)
	Dry	Rainy							
Santa Maria	O	O	16.70 (2.97) 14.60–18.80	2.65 (2.33) 1.00–4.30	6.67 (0.35) 6.42–6.92	40.65 (1.48) 39.60–41.70	8.11 (0.91) 7.47–8.75	22.16 (0.65) 21.70–22.62	Mud
Melissa	O	E	17.75 (6.15) 13.40–22.10	1.00 (0) 1.00–1.00	6.64 (0.42) 6.34–6.94	32.55 (2.62) 30.70–34.40	8.66 (1.27) 7.76–9.55	13.53 (4.05) 10.67–16.40	Mud
Mourão	O	O	21.10 (5.94) 16.90–25.30	1.50 (0.71) 1.00–2.00	7.25 (1.16) 6.43–8.07	21.51 (2.53) 19.72–23.30	8.62 (0.37) 8.35–8.88	17.67 (0.74) 17.14–18.20	Fine sand
Rio dos Patos	O	E	17.85 (6.15) 13.50–22.20	2.00 (0.71) 1.50–2.50	6.58 (0.53) 6.20–6.95	40.85 (9.69) 34.00–47.70	8.05 (0.52) 7.68–8.42	10.05 (0.87) 9.43–10.66	Mud
Harmonia	O	O	20.35 (4.74) 17.00–23.70	2.25 (1.06) 1.50–3.00	7.16 (1.05) 6.42–7.90	28.85(3.04) 26.70–31.00	10.1 (1.1) 9.30–10.87	3.70 (0.30) 3.49–3.92	Fine sand
Alagados	O	O	19.70 (5.52) 15.80–23.60	2.00 (0) 2.00–2.00	7.47 (0.66) 7.00–7.94	40.10 (2.97) 38.00–42.20	8.53 (1.48) 7.48–9.57	2.24 (1.09) 1.47–3.01	Seixos
Julio Mesquita Filho	O	E	20.10 (4.81) 16.70–23.50	2.10 (1.56) 1.00–3.20	6.72 (0.50) 6.36–7.07	37.75 (3.89) 35.00–40.50	8.62 (0.34) 8.38–8.86	17.14 (1.62) 15.99–18.29	Very fine sand
Salto Santiago	O	O	18.90 (0) 18.90–18.90	30.00 (0) 30.00–30.00	7.03 (0) 7.03–7.03	39.70 (0) 39.70–39.70	9.36 (0) 9.36–9.36	15.10 (3.26) 12.80–17.41	Mud
Salto Caxias	O	O	21.00 (3.39) 18.60–23.40	27.00 (33.94) 3.00–51.00	6.75 (0.71) 6.25–7.25	36.90 (3.82) 34.20–39.60	8.07 (0.08) 8.01–8.12	12.85 (2.31) 11.21–14.48	Medium sand
Piraquara	O	O	20.15 (5.44) 16.30–24.00	2.15 (0.92) 1.50–2.80	2.80 (0.51) 6.11–6.83	23.40 (0.71) 22.90–23.90	8.08 (1.60) 6.95–9.21	10.42 (4.81) 7.02–13.82	Medium sand
Irai	E	E	20.05 (6.29) 15.60–24.50	1.65 (0.21) 1.50–1.80	6.87 (0.21) 16.30–7.02	50.90 (1.41) 49.90–51.90	7.56 (1.46) 6.52–8.59	15.60 (2.43) 13.88–17.31	Mud
Passaúna	O	O	20.00 (5.80) 15.90–24.10	1.25 (0.35) 1.00–1.50	8.36 (0.76) 7.82–8.90	126.80 (2.69) 124.90–128.70	6.91 (1.77) 5.65–8.16	11.86 (0.15) 11.76–11.96	Medium sand
Jordão	O	O	20.60 (2.26) 19.00–22.20	6.75 (7.42) 1.50–12.00	6.98 (0) 6.98–6.98	23.80 (0) 23.80–23.80	7.35 (5.80) 7.35–7.35	38.81 (18.11) 26.00–51.62	Coarse sand
Salto do Vau	O	O	16.10 (5.09) 12.50–19.70	2.00 (0) 2.00–2.00	6.33 (0.29) 6.12–6.53	21.15 (2.48) 19.39–22.90	9.41 (0.77) 8.86–9.95	10.52 (0.17) 10.39–10.64	Fine sand
Cavernoso	O	O	20.05 (4.88) 16.60–23.50	0.85 (0.21) 0.70–1.00	7.27 (0.34) 7.03–7.51	31.65 (2.19) 30.10–33.20	8.16 (0.21) 8.01–8.30	17.58 (4.39) 14.48–20.68	Very fine sand
Salto Segredo	O	O	20.85 (2.62) 19.00–22.70	1.50 (0.71) 1.00–2.00	6.33 (0.13) 6.23–6.42	36.95 (5.30) 33.20–40.70	7.82 (0.27) 7.63–8.01	13.62 (1.60) 12.48–14.75	Mud
Foz do Areia	O	O	21.05 (5.16) 17.40–24.70	1.95 (2.19) 0.40–3.50	7.13 (1.27) 6.23–8.02	37.70 (2.83) 35.70–39.70	8.27 (1.77) 7.02–9.52	13.48 (1.62) 12.33–14.62	Coarse sand
Salto Osório	O	O	21.55 (3.61) 19.00–24.10	1.35 (0.21) 1.20–1.50	7.35 (1.63) 6.20–8.50	36.75 (2.76) 34.80–38.70	8.93 (0.95) 8.25–9.60	12.45 (1.30) 11.53–13.38	Medium sand
Curucaca	O	O	18.25 (7.00) 13.30–23.20	0.60 (0.28) 0.40–0.80	6.68 (0) 6.68–6.68	31.30 (0) 31.30–31.30	7.84 (0) 7.84–7.84	14.83 (5.46) 10.97–18.69	Pebbles
Chavantes	O	O	22.05 (4.60) 18.80–25.30	4.75 (0.35) 4.50–5.00	7.09 (0.28) 6.89–7.28	53.85 (6.29) 49.40–58.30	7.78 (0.78) 7.22–8.33	1.96 (2.04) 0.52–3.40	Very fine sand
Salto Grande	O	O	21.90 (5.37) 18.10–25.70	2.50 (0.42) 2.20–2.80	6.66 (0.47) 6.33–6.99	59.30 (4.81) 55.90–62.70	7.38 (1.02) 6.66–8.10	8.35 (10.61) 0.85–15.85	Mud
Capivara	O	O	23.95 (5.59) 20.00–27.90	3.75 (2.47) 2.00–5.50	7.21 (0.66) 6.74–7.67	58.95 (1.48) 57.90–60.00	7.84 (0.26) 7.65–8.02	7.46 (4.43) 4.33–10.59	Very fine sand
Canoas II	O	O	23.70 (5.80) 19.60–27.80	0.45 (0.07) 0.40–0.50	7.24 (0.34) 7.00–7.48	59.50 (2.55) 57.70–61.30	8.29 (0.47) 7.95–8.62	13.62 (6.74) 8.85–18.38	Very fine sand
Canoas I	O	O	23.85 (5.59) 19.90–27.80	0.45 (0.07) 0.40–0.50	6.98 (0.64) 6.53–7.43	60.75 (3.61) 58.20–63.30	8.20 (1.21) 7.34–9.05	8.75 (3.28) 6.43–11.07	Fine sand
Taquaruçu	O	O	23.25 (5.02) 19.70–26.80	2.25 (1.06) 1.50–3.00	7.14 (0.03) 7.12–7.16	57.50 (0.57) 57.10–57.90	8.15 (1.12) 7.35–8.94	11.67 (6.10) 7.36–15.99	Fine sand
Rosana	O	O	24.15 (5.30) 20.40–27.90	1.50 (0) 1.50–1.50	7.39 (0.27) 7.20–7.58	58.10 (0.28) 57.90–58.30	7.81 (1.29) 6.90–8.72	8.14 (10.08) 1.01–15.27	Medium sand
Parigot de Souza	O	O	20.50 (4.53) 17.30–23.70	2.15 (0.92) 1.50–2.80	7.30 (0.83) 6.71–7.88	60.75 (4.60) 57.50–64.00	7.99 (0.37) 7.72–8.25	5.74 (0.79) 5.19–6.30	Medium sand
Vossoroca	O	M	19.20 (4.81) 15.80–22.60	1.30 (0.71) 0.80–1.80	6.72 (1.02) 6.00–7.44	37.70 (2.97) 35.60–39.80	8.49 (0.72) 7.98–9.00	8.60 (0.98) 7.90–9.29	Medium sand
Salto do Meio	O	O	18.25 (3.46) 15.80–20.70	3.50 (0.71) 3.00–4.00	6.74 (0.16) 6.62–6.85	38.25 (0.78) 37.70–38.80	9.29 (0.95) 8.62–9.96	15.62 (3.05) 13.46–17.78	Mud
Guaricana	M	O	20.05 (6.29) 15.60–24.50	5.75 (6.01) 1.50–10.00	6.21 (0.71) 5.70–6.71	25.75 (1.91) 24.40–27.10	9.84 (0.83) 9.25–10.43	17.53 (5.73) 13.48–21.59	Mud

Appendix 2. Mean values, standard deviation (between parentheses), minimum and maximum of the physical and chemical variables of the water and sediment and organic content in the profundal zones of the reservoirs. O, Oligotrophic; M, Mesotrophic; E, Eutrophic.

Reservoirs profundal	Period		Water temperature (°C)	Depth (m)	pH	Electrical conductivity (µS.cm^{-1})	Dissolved oxygen (mg.L^{-1})	Organic content (%)	Sediment (> %)
	Dry	Rainy							
Santa Maria	O	O	16.05 (3.46) 13.60–18.50	4.40 (0.14) 4.30–4.50	6.69 (0.49) 6.34–7.03	39.80 (3.25) 37.50–42.10	8.33 (0.25) 8.15–8.50	23.89 (0.44) 23.58–24.20	Mud
Melissa	O	E	17.70 (6.22) 13.30–22.10	5.15 (0.21) 5.00–5.30	6.50 (0.44) 6.19–6.81	32.65 (2.62) 30.80–34.50	8.49 (1.01) 7.77–9.20	19.65 (1.09) 18.88–20.42	Mud
Mourão	O	O	19.00 (5.09) 15.40–22.60	12.25 (1.06) 11.50–13.00	6.34 (0.64) 5.88–6.79	24.25 (4.17) 21.30–27.20	3.38 (2.17) 1.84–4.91	20.69 (1.58) 19.57–21.81	Medium sand
Rio dos Patos	O	E	18.10 (6.51) 13.50–22.70	5.63 (0.18) 5.50–5.75	6.73 (0.40) 6.44–7.01	41.00 (9.48) 34.30–47.70	7.43 (1.12) 6.64–8.22	4.27 (0.67) 3.80–4.74	Medium sand
Harmonia	O	O	14.40 (1.13) 13.60–15.20	12.75 (1.06) 12.00–13.50	5.90 (0.54) 5.51–6.28	45.15 (22.42) 29.30–61.00	1.09 (1.54) 1.09–2.18	17.52 (0.03) 17.50–17.54	Coarse sand
Alagados	O	O	18.60 (4.81) 15.20–22.00	9.25 (0.35) 9.00–9.50	6.84 (0.13) 6.74–6.93	41.20 (3.68) 38.60–43.80	5.16 (4.76) 1.79–8.52	16.88 (2.53) 15.09–18.66	Mud
Julio Mesquita Filho	O	E	20.00 (4.67) 16.70–23.30	6.00 (0) 6.00–6.00	6.97 (0.53) 6.59–7.34	43.00 (11.74) 34.70–51.30	8.09 (0.58) 7.68–8.50	18.60 (0.78) 18.04–19.15	Very fine sand
Salto Santiago	O	O	16.00 (0.28) 15.80–16.20	76.00 (2.83) 74.00–78.00	6.43 (0.62) 5.99–6.86	49.55 (8.56) 43.50–55.60	1.67 (2.23) 0.09–3.25	18.67 (1.56) 17.57–19.78	Coarse sand
Salto Caxias	O	O	17.95 (1.48) 16.90–19.00	52.65 (0.49) 52.30–53.00	6.48 (0.37) 6.22–6.74	38.90 (6.65) 34.20–43.60	5.66 (2.17) 4.12–7.19	16.94 (2.40) 15.24–18.64	Medium sand
Piraquara	O	O	16.30 (1.27) 15.40–17.20	18.00 (0) 18.00–18.00	5.90 (0.07) 5.85–5.95	25.95 (2.62) 24.10–27.80	3.48 (3.57) 0.95–6.00	24.38 (1.61) 23.24–25.51	Mud
Irai	E	E	17.95 (3.04) 15.80–20.10	8.25 (0.35) 8.00–8.50	6.66 (0.29) 6.45–6.86	50.35 (4.03) 47.50–53.20	3.85 (5.27) 0.12–7.57	36.88 (3.00) 34.76–39.01	Mud
Passaúna	O	O	16.00 (0.28) 15.80–16.20	14.25 (0.35) 14.00–14.50	8.08 (0.37) 7.82–8.34	141.85 (18.60) 128.70–155.00	2.83 (4.00) 0–5.65	22.88 (1.22) 22.02–23.74	Mud
Jordão	O	O	11.85 (0.35) 11.60–12.10	59.50 (0.71) 59.00–60.00	6.50 (0.78) 5.94–7.05	78.45 (23.12) 62.10–94.80	0.04 (0.06)–0.08–0.08	38.81 (18.11) 26.00–51.62	Coarse sand
Salto do Vau	O	O	15.90 (4.95) 12.40–19.40	3.78 (0.04) 3.75–3.80	6.29 (0.76) 5.75–6.82	21.55 (2.33) 19.90–23.20	7.20 (1.42) 6.19–8.20	1.72 (1.07) 0.96–2.47	Fine sand
Cavernoso	O	O	19.35 (5.02) 15.80–22.90	8.05 (0.35) 7.80–8.30	7.06 (0.34) 6.82–7.30	32.15 (2.33) 30.50–33.80	7.88 (0.01) 7.87–7.88	52.72 (25.81) 34.47–70.97	Mud
Salto Segredo	O	O	13.95 (0.49) 13.60–14.30	100.00 (0) 100.0–100.0	6.34 (0.75) 5.81–6.87	33.75 (3.18) 31.50–36.00	4.85 (4.04) 1.99–7.71	19.23 (0.71) 18.73–19.73	Coarse sand
Foz do Areia	O	O	12.30 (0.14) 12.20–12.40	135.00 (0) 135.0–135.0	5.75 (0.01) 5.74–5.76	59.75 (2.47) 58.00–61.50	0.74 (0.97) 0.05–1.42	17.77 (2.23) 16.19–19.35	Coarse sand
Salto Osório	O	O	18.70 (0.42) 18.40–19.00	42.50 (0.71) 42.00–43.00	6.58 (0.62) 6.14–7.02	38.40 (4.24) 35.40–41.40	6.15 (1.17) 5.32–6.97	16.73 (0) 16.73–16.73	Coarse sand
Curucaca	O	O	17.00 (5.23) 13.30–20.70	11.25 (1.06) 10.50–12.00	6.63 (0.33) 6.40–6.86	28.85 (6.29) 24.40–33.30	7.14 (1.00) 6.43–7.84	22.86 (0.52) 22.49–23.23	Mud
Chavantes	O	O	18.30 (0.57) 17.90–18.70	66.50 (16.26) 55.00–78.00	6.43 (0.23) 6.26–6.59	57.85 (4.60) 54.60–61.10	4.00 (3.87) 1.26–6.74	9.63 (3.32) 7.28–11.97	Medium sand
Salto Grande	O	O	21.35 (5.02) 17.80–24.90	9.60 (0.57) 9.20–10.00	6.94 (0.21) 6.79–7.08	61.35 (7.28) 56.20–66.50	6.99 (1.14) 6.18–7.79	10.04 (9.00) 3.68–16.40	Mud
Capivara	O	O	19.35 (2.90) 17.30–21.40	51.75 (1.06) 51.00–52.50	6.79 (0.44) 6.48–7.10	57.25 (2.19) 55.70–58.80	3.25 (4.21) 0.27–6.23	20.79 (7.48) 15.50–26.08	Medium sand
Canoas II	O	O	21.85 (4.45) 18.70–25.00	16.50 (0) 16.50–16.50	7.01 (0.16) 6.90–7.12	61.80 (0.85) 61.20–62.40	6.86 (1.23) 5.99–7.73	16.31 (0.49) 15.97–16.65	Mud
Canoas I	O	O	22.35 (4.74) 19.00–25.70	26.50 (0.71) 26.00–27.00	6.82 (0.17) 6.70–6.94	61.85 (3.75) 59.20–64.50	6.21 (1.75) 4.97–7.44	17.29 (0.44) 16.98–17.60	Mud
Taquaruçu	O	O	21.40 (3.25) 19.10–23.70	26.75 (0.35) 26.50–27.00	7.04 (0.15) 6.93–7.14	56.60 (1.41) 55.60–57.60	7.14 (1.45) 6.11–8.16	9.16 (6.73) 4.40–13.92	Medium sand
Rosana	O	O	22.75 (4.45) 19.60–25.90	25.50 (0.71) 25.00–26.00	7.00 (0.13) 6.91–7.09	59.40 (0.85) 58.80–60.00	6.83 (1.59) 5.70–7.95	7.37 (0.62) 6.93–7.80	Medium sand
Parigot de Souza	O	O	14.75 (0.21) 14.60–14.90	40.00 (4.24) 37.00–43.00	6.52 (0.11) 6.44–6.59	64.20 (4.24) 61.20–67.20	0.08 (0.02) 0.06–0.09	16.09 (1.40) 15.10–17.09	Coarse sand
Vossoroca	O	M	14.35 (0.35) 14.10–14.60	11.75 (1.06) 11.00–12.50	6.03 (0.27) 5.84–6.22	39.60 (0.71) 39.10–40.10	2.04 (2.84) 0.03–4.04	15.40 (0.62) 14.96–15.84	Medium sand
Salto do Meio	O	O	18.30 (3.25) 16.00–20.60	6.60 (0.57) 6.20–7.00	6.74 (0.40) 6.45–7.02	37.60 (0.71) 37.10–38.10	8.38 (0.09) 8.31–8.44	20.21 (2.00) 18.80–21.62	Mud
Guaricana	M	O	15.35 (3.32) 13.00–17.70	14.50 (3.54) 12.00–17.00	5.70 (0.49) 5.35–6.04	28.10 (0.28) 27.90–28.30	5.82 (1.61) 4.68–6.95	18.15 (0.95) 17.48–18.82	Mud